Resistance in Durum Wheat Sources to Hessian Fly (Diptera: Cecidomyiidae) Populations in Eastern USA

R. H. Ratcliffe,* F. L. Patterson, S. E. Cambron, and H. W. Ohm

ABSTRACT

Damage from Hessian fly, *Mayetiola destructor* (Say), infestation of soft red winter wheat, *Triticum aestivum* L, in the eastern USA has been reduced by the deployment of genes for resistance in commercial cultivars. Hessian fly populations in the eastern USA have developed virulence to previously deployed genes for resistance except for *H*13, deployed in 1998. Durum wheat, *Triticum durum* Desf., is an important source of resistance to Hessian fly. Four populations of Hessian fly, believed representative of the eastern USA, were selected for seedling tests of 26 durum genotypes which had shown resistance to Hessian fly biotypes B, D, or L in earlier laboratory tests. The putative number of genes conditioning resistance to laboratory biotype L was determined in backcross segregation analysis of 11 PI selections of unknown genotype. The number of genes for resistance to Hessian fly was also recorded of other durum genotypes in the test from observed segregation or published data. Some common wheat genotypes were included in tests with the four populations. Most of the 26 durum genotypes were resistant to the four eastern USA Hessian fly populations. The four Hessian fly populations were similar in avirulence to most durum germplasm lines but with differences in virulence to a few lines. The four populations were virulent to the previously deployed resistances provided by *H*3, *H*5, and *H*6. The northern two Hessian fly populations were virulent and the southern two populations were avirulent to the previously deployed resistance of *H*7*H*8. Resistance to laboratory biotypes D or L of the 26 durum genotypes was conditioned by one, two, or three genes, depending upon line.

DURUM WHEAT GERMPLASM, especially from the Mediterranean region, is an important source of genes for resistance to Hessian fly. Once Hessian fly resistance is identified in durum wheats, it seems prudent to test accessions for resistance to a number of fly biotypes or populations to identify those that are potentially useful in breeding resistant common wheat cultivars (Cambron et al., 1995). This approach has been utilized with Hessian fly biotypes (Patterson et al., 1994), but until recently not with Hessian fly populations representative of those found in the eastern USA.

During the 1990s, 87 Hessian fly populations from the eastern USA soft winter wheat region were evaluated for biotype composition (Ratcliffe et al., 1994, 1996, 2000, unpublished data, 2000). These populations were broadly grouped into five areas; northeast (New York and Pennsylvania), mid-Atlantic (Delaware, Maryland, North Carolina, and Virginia), southeast (Florida, Georgia, and South Carolina), mid-south (Alabama, Arkansas, Louisiana, Mississippi, and Tennessee), and Midwest (Illinois, Indiana, Michigan, Missouri, and Ohio). In addition to testing field populations for biotype composition, selected populations were increased and maintained for testing against wheat germplasms and cultivars being developed in the Purdue soft winter wheat breeding program (Ratcliffe, 2000). Hessian fly populations selected for further testing were considered representative of those collected within specific regions of the eastern USA.

Previous tests of wheat germplasms with Hessian fly resistance included lines in both common (soft and hard winter wheat) and durum backgrounds and with deployed and undeployed resistance genes (Ratcliffe et al., 1994, 1996, 2000). Hessian fly populations from the southeastern USA demonstrated the greatest range in virulence to both deployed and undeployed resistance genes and populations from the mid-Atlantic area demonstrated the highest frequency of virulence to undeployed genes, particularly *H*13. In contrast, fly populations from the mid-south and Midwest were relatively uniform in biotype composition (primarily biotype L) and demonstrated less virulence to undeployed genes. Hessian fly incidence in northeastern states was very low during the 1990s and consequently insufficient data were collected during this time on biotype composition to be of value. Because of limited seed supply of many of the wheat lines reported herein, tests were conducted on only four Hessian fly populations collected in 1999 from the mid-Atlantic and southeastern states. These were considered representative of eastern USA populations demonstrating greatest diversity in virulence to resistance genes, as described above.

The rationale for determining gene number conditioning resistance to Hessian fly biotypes D or L in relation to resistance to eastern USA populations is that the same genes may be effective for both. This relationship appears most clear where there is only one gene for resistance to biotype D or L and where resistance to one or more eastern USA populations occurs. Where two or more genes condition resistance to biotype D or L, then at least one may provide resistance to the eastern USA populations. Hessian fly biotype D is virulent on wheat genotypes with deployed resistance genes *H*3, *H*6, or *H*7*H*8, but not on those with gene *H*5. Biotype L is virulent on wheat genotypes with any of

R.H. Ratcliffe and S.E. Cambron, USDA-ARS, Crop Production and Pest Control Research Unit, W. Lafayette, IN 47907; F.L. Patterson and H. W. Ohm, Dep. of Agronomy, Purdue Univ., W. Lafayette, IN 47907. This is a joint contribution of the USDA-ARS and Purdue Univ. Agric. Res. Programs and has been approved for publication as Journal Article No. 16613 of the Purdue Univ. Agric. Res. Programs. This article presents the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation by USDA or Purdue Univ. Received 23 Aug. 2001. *Corresponding author (roger_ratcliffe@entm.purdue.edu).

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Abbreviations: CI, a number assigned by the former Division of Cereal Crops and Diseases, GRIN, Germplasm Resources Information Network; PI, plant identification number of the USDA-ARS National Small Grains Collection, Aberdeen, ID.

the above deployed genes. Neither biotype D or L is virulent on wheat genotypes with recently deployed *H*13.

The objectives of this research were to (i) use 26 durum wheat genotype reactions to evaluate similarities and differences in virulence among four eastern USA Hessian fly populations, (ii) determine which durum germplasm lines offered the best potential usefulness as sources of resistance to the four Hessian fly populations, and (iii) determine the number of genes conditioning resistance to laboratory biotype L of Hessian fly in 11 durum wheat PI lines for which gene number was not known.

MATERIALS AND METHODS

Hessian Fly Populations

Wheat selections were tested for resistance to Hessian fly populations from Sussex County Delaware, Spalding County Georgia, Wicomico County Maryland, and Barnwell County South Carolina. Collection information and biotype composition of the four Hessian fly populations are summarized in Table 1. Cooperators in the four states (see Acknowledgments) collected wheat samples from which Hessian flies were retrieved. Wheat samples were sent to the USDA-ARS laboratory at West Lafayette, IN, and were processed and fly populations increased for evaluation as described by Ratcliffe et al. (1994). Following increase and determination of biotype composition, fly populations were stored in the flaxseed stage (onset of darkening of the 2nd instar integument) at 5°C until needed for further research (Ratcliffe et al., 1994).

Evaluating Resistance

Forty wheat lines (26 durum and 14 common) were grown in greenhouse flats (36 by 54 by 8 cm) as described by Cartwright and LaHue (1944) for testing against fly populations. Only data for the durum lines and seven common wheat selections are reported in this paper. The 40 selections were seeded in four sets of four flats each, one set per fly population. Test flats were set up with 12 rows (each 17.5 cm) spaced 2 cm apart. Rows 1 through 5 and 8 through 12 were seeded to wheat lines and rows 6 through 7 to five wheat cv. Monon (*H*3), Magnum (*H*5), Caldwell (*H*6), Seneca (*H*7*H*8), and INW9811 (*H*13) and one germplasm line 'Lola' (*H*12) that served as controls or as differentials for defining Hessian fly biotypes, as described below. Rows 5 through 6 were divided in thirds to accommodate the six controls. Wheat lines were seeded at the rate of 23 through 37 seeds per row (depending upon seed availability per line) and the controls at the rate of 20 seeds per one-third row. Flats were placed under a cheesecloth tent (1-mm mesh, ≈12 cm from top of plants to cheesecloth) when plants were in the two-leaf stage and were infested with ≈300 gravid females for 3 to 4 d, after which the tent was removed. To eliminate cross contamination of populations, plants in flats infested with each population were isolated until adults were dead. Flats were held in growth chambers at 18°C and a photoperiod of 12:12 (L:D) h throughout the test. Illumination within chambers was approx. 650 to 700 μmol m^{-2} s^{-1}. Plant response to larval infestation was recorded after 19 to 21 d. All plants were removed from the flat, rated as susceptible or resistant, and dissected to determine the presence or absence of larvae, larval survival and approximate stage of development of living larvae.

Data were recorded as the number of resistant and susceptible plants for each entry and converted to percentage resistant or susceptible plants per entry. The relative resistance or susceptibility of wheat lines/cultivars was expressed as *resistant* (90–100% resistant plants), *moderately resistant* (76–89% resistant plants), or *susceptible* (0–75% resistant plants). A Hessian fly population was expressed as *virulent* to a wheat selection when 25% of the plants within the selection were susceptible to the fly population.

Table 1. Collection information and biotype composition of Hessian fly populations from Delaware, Maryland, Georgia, and South Carolina tested against durum wheat lines.

State, region†	Year collected	Biotype composition
		%
Delaware, ES	1999	L=85; J=7; D=5; B=3
Maryland, ES	1999	L=96; D=4
Georgia, WC	1999	O=25; E=25; G=19; M=9; F=6; GP, D, L=4; B, H, J=2
South Carolina, SW	1999	G=47; O=32; E=11; M=8; GP, N=1

† Region of state: ES = Eastern Shore, WC = West central; SW = Southwest.

Sources of Resistant Germplasm

Most of the durum lines resistant to Hessian fly biotypes D and L were identified in tests by personnel of the USDA-ARS, Crop Production and Pest Control Research Unit at Purdue University in cooperation with the USDA-ARS National Small Grains and Potato Germplasm Research Unit, Aberdeen, ID. The country of origin and other information on this group of germplasm lines was provided from records of the USDA-ARS, National Germplasm Resources Laboratory, Beltsville, MD (Table 2).

Lines with Previously Known Gene Number

The number of genes conditioning resistance to Hessian fly in 15 of the 26 lines was obtained from published research or

Table 2. Some durum wheat sources of resistance to populations of Hessian fly collected in eastern USA.

Source	Additional information†	Origin†
Port 2536		Portugal
Port 2852		Portugal
Rebeiro	CI 1755	Portugal
CI 3146	Alai Beriole Glabre	Tunisia
CI 3984		Tunisia
CI 7041	PI 56233	Portugal
CI 7066	Tremez Rojo	Portugal
CI 7535	PI 61862	Morocco
CI 7539	P61886	Morocco
CI 15160	Dimini Lesvon	Greece
PI 134942		Portugal
PI 166497	Yaz	Turkey
PI 185410	Perdaleiro	Portugal
PI 185721	Branco	Portugal
PI 192351	Amarelo de Barba Branca	Portugal
PI 192738	Vermelho Fino	Portugal
PI 192839	Tremes Rijo	Portugal
PI 192840	Tremes Rijo	Portugal
PI 192851	Tremes Preto	Portugal
PI 274681	Muriciense	Poland
PI 323440		Austria
Jori		Morocco
Giorgio331		Italy
P80164H5-2-9 (*H*16)	Derived from PI 94587	Purdue University
PI428435 (*H*17)	BD141BW28	Russia
P84702H12-1-3 (*H*19)	Derived from PI 422297	Purdue University

† Most of the information is from the Germplasm Resources Information Network (GRIN) program conducted by the USDA-ARS National Small Grains Germplasm Research Staff, Aberdeen, ID. PI is the plant identification number. CI is a number assigned by the former Division of Cereal Crops and Diseases, USDA.

Table 3. Reactions of durum wheat lines to Hessian fly populations from eastern USA.

Source	Plants resistant to Hessian fly populations from				Putative number of genes for resistance	
	MD	DE	SC	GA	No.	Test biotype
	%					
Durum wheat						
Port 2536	100	100	100	100	3	D
Port 2852	100	100	100	100	2	D
Rebeiro	100	100	100	100	1	D
CI 3146	100	100	100	100	1	D
CI 3984	100	100	85	100	1	D
CI 7041	100	100	100	100	2	D
CI 7066	100	100	100	100	2	D
CI 7535	100	100	100	100	3	D
CI 7539	94	100	100	92	2	D
CI 15160	100	100	100	100	3	D
PI 134942	100	100	100	100	2	L
PI 166497	100	100	100	96	2	L
PI 185410	100	100	100	100	1	L
PI 185721	100	100	100	100	1	L
PI 192351	95	100	100	100	2	L
PI 192738	100	100	100	100	1	L
PI 192839	100	100	100	100	2	L
PI 192840	100	100	100	100	3	L
PI 192851	100	94	100	100	1	L
PI 274681	95	100	100	100	2	L
PI 323440	100	100	100	100	1	L
Jori (*H*20)	96	100	100	100	1	D
Giorgio 331	100	94	100	100	1	D
P80164H5 (*H*16)	100	100	100	100	1	D
PI 428435 (*H*17)	58	83	100	100	1	D
P84702H12 (*H*19)	100	100	84	95	1	D
Common wheat						
P921682A4 (*H*16)	100	89	100	–	1	D
Lola (*H*12)	44	73	80	93	1	D
INW9811 (*H*13)	97	98	92	100	1	D
Monon (*H*3)†	0	3	0	2	1	C
Magnum (*H*5)†	2	2	30	14	1	D
Caldwell (*H*6)†	6	9	10	40	1	B
Seneca (*H7H*8)†	2	5	99	97	2	E

† There are four differentials with genes to identify the 16 biotypes of Hessian fly, GP and A to O. The genes have been previously deployed in cultivars in eastern USA.

from our unpublished data, as described below. This information also is shown in Table 3 for purposes of comparison with segregation data for the 11 PI lines reported herein. In some cases,the number of genes for resistance among the 15 lines was deduced by segregation analysis in backcross populations designed to develop single gene resistant lines in durum or common wheat for breeding or research. The 15 lines are placed in three groups for ease of description.

Morocco Lines

Port 2536, Port 2852, and Rebeiro were obtained for research at Purdue University by M. Obanni from his previous research in Morocco (Obanni et al., 1989). Rebeiro durum wheat in Morocco was selected from a mixture of durum and common wheat in a seed lot of CI 1755 obtained from the USDA-ARS National Small Grains Collection then located in Beltsville, MD. Resistance in Port 2536, Port 2852,and Rebeiro was conditioned by three, two, and one gene, respectively (Ohm, Patterson, unpublished data 1995).

Seven CI Lines

Five lines, CI 3146 to CI 7535 (Table 3) previously were evaluated for number of genes for resistance to Hessian fly biotypes D or L at 19 or 21°C, for resistance interrelationships, and for their differences from known resistant tester stocks with genes *H*5, *H*9, *H*14, or *H*16 (Cambron et al., 1995). Germplasm line CI 7539 previously was tested to biotype L in backcross populations; germplasm line CI 15160 was derived from a progeny of CI 15160 that had better resistance to biotype L at 25°C. Resistance was conditioned by one gene in CI 3146 (Cambron et al., 1995) and CI 3984 (Ohm, Patterson, unpublished data, 1995), two genes in CI 7041 and CI 7066 (Cambron et al., 1995) and CI 7539 (Ohm, Patterson, unpublished data, 1995), and three genes in CI 7535 (Cambron et al., 1995) and CI 15160 (Ohm, Patterson, unpublished data, 1995). The single genes conditioning resistance to Hessian fly biotype L in CI 3146 and in CI 3984 appear to be alleles based on results of testcross F_2 family analysis (Ohm, Patterson, unpublished data, 1995) and different reactions to Hessian fly populations in this study and in a field test at Griffin, GA (J.J. Johnson, personal communication, 2000).

Five Additional Lines

Five lines were selected from germplasm demonstrating resistance in tests conducted at Manhattan, KS (Jori), and West Lafayette, IN (Giorgio 331, PI 428435, P80164H5, and P84702H12). Resistance was conditioned by one gene in each of the five lines as follows; Jori (Amri et al., 1990), PI 428435 (Obanni et al., 1988), P80164H5 and P84702H12 (Patterson et al., 1994), and Giorgio 331 (Ohm, Patterson, unpublished data, 1995). P80164H5 (*H*16) and P84702H12 (*H*19) each resulted from one backcross of the resistance gene donor line to susceptible durum line D6647 (Lebsock et al., 1972).

Lines with Unknown Gene Number

Eleven durum germplasm lines, PI 134942 to PI 323440 (Table 3), were selected for study from a group of 50 resistant lines based on resistance to biotype L at 25°C (Unpublished data, 1995). The 50 resistant lines were identified among a group of lines from the USDA-ARS National Small Grains Collection by USDA-ARS and Purdue University personnel as part of the Germplasm Resources Information Network (GRIN) initiative.

Common Wheat Selections

Common wheat selections compared with durum lines were germplasm lines P921682A4, Lola, and the cv. INW9811. P921682A4 (*H*16) was selected following six backcrosses of P80164H5 (*H*16) durum germplasm line to 'Newton' (CI 17715) common wheat (Patterson et al., 1988). Lola (*H*12) was selected from the backcross Newton*4/'Luso' (Patterson et al., 1994). Luso common wheat was shown to have one gene which conditioned resistance to biotypes B and D at 20°C (Oellermann et al., 1983). Resistance gene *H*12 has not been deployed for resistance to Hessian fly in cultivars in the USA. INW9811 (*H*13) is a soft red winter wheat cultivar released by Purdue University and the USDA-ARS in 1998 for production in the eastern USA (Ratcliffe et al., 2000). Resistance was derived from *Triticum tauschii* (Coss) Schmal. (Martin et al., 1982). *H*13 was mapped on chromosome 6D of wheat (Gill et al., 1987). The *H*13 gene conditions excellent resistance to Hessian fly biotypes D and L at temperatures of 19 to 25°C. Lola and INW9811 previously were evaluated for resistance to Hessian fly populations collected from the mid-Atlantic and southeastern USA in the late 1980s and mid-nineties, respectively (Ratcliffe et al., 1994, 2000). The four differential cultivars used in defining Hessian fly biotypes were Monon, Magnum, Caldwell, and Seneca. These cultivars have been deployed in the eastern USA and these genes for resistance have been deployed in other cultivars as well, beginning

with Seneca (CI 12529, *H7H8*) in 1949, 'Dual' (CI 13083, *H3*) in 1955, 'Knox 62' (CI 13701, *H6*) in 1962, and 'Arthur 71' (CI 15282, *H3H5*) in 1971.

Estimating Number of Genes Conditioning Resistance

The Chi-square goodness-of-fit test with adjustment for small numbers (Steel and Torrie, 1980) was used to estimate the number of genes conditioning resistance to Hessian fly biotypes D and L. Analyses were based on reactions of F_2 families from backcross or testcross tests. In most cases 80 or 90 families, parents, and check plants were grown in 10 greenhouse flats and infested with Hessian fly and placed in a growth chamber for 19 to 21 d before determining plant reactions. A family was represented by about 25 or 30 plants. Pure biotypes D or L were used. Biotype L is the more virulent biotype. In tests of a germplasm line, materials were derived from the progeny of a single typical selfed plant then tested for resistance to Hessian fly. In classifying backcross or testcross F_2 families, the distinction was between those families segregating for resistant and susceptible plants and those families where all plants were susceptible.

Resistant Reactions of Heterozygous Plants

Resistance of wheat to Hessian fly is expressed most often as partial dominance. The method suggested by Obanni et al. (1988) was used to estimate the expression of resistance of plants heterozygous for a single gene for resistance. In those backcross families segregating for a single factor, a 1:2:1 ratio of homozygous resistant (RR) to heterozygous (Rr) to susceptible (rr), F_2 plants is expected. The homozygous resistant F_2 plants should express resistance similar to plants of the resistant parent. The number of resistant and the number of susceptible F_2 plants within segregating families were summed. An example is presented to illustrate the method. With 400 F_2 plants total, 100 would be expected to be RR, 200 to be Rr, and 100 rr. If the total number of resistant F_2 plants was 200 then 200 minus 100 RR plants leaves 100 Rr, i.e., 50% of the heterozygous plants expressed resistance.

RESULTS

Hessian Fly Resistance

Results of tests with Hessian fly populations and wheat selections are summarized in Table 3. Twenty-five of the 26 durum lines were resistant or moderately resistant (84–100% resistant plants) to the four populations. The exception, PI 428435, was susceptible to the Maryland population (58% resistant plants), moderately resistant to the Delaware population (83% resistant plants), and resistant to populations from Georgia and South Carolina. Common wheat selection P9216-82A4 was resistant to populations from Maryland and South Carolina and moderately resistant to the Delaware population. Data for the response of P921682A4 to the Georgia population are not shown in Table 3 because results were erroneous, probably because of a mix-up in seed before planting. INW9811 was resistant to all fly populations, while Lola was resistant and moderately resistant to fly populations from Georgia and South Carolina, respectively, but susceptible to Maryland and Delaware populations. The response of the differentials was as expected on the basis of the biotype composition of the four fly populations (Table 1). Monon, Magnum, and Caldwell were susceptible to all populations, while Seneca was resistant to the Georgia and South Carolina populations, but susceptible to those from the mid-Atlantic area.

There was 100% mortality of larvae observed on resistant plants of 18 of the 26 durum lines. This included Port 2536, Port 2852, Rebeiro, CI 3984, CI 7041, CI 7066, CI 7535, CI 15160, PI 134942, PI 166947, PI 185410, PI 185721, PI 192839, PI 192840, PI 192851, PI 323440, Jori, and P80164H5. There were living and dead larvae on some plants of CI 3146 and PI 192738 although all plants were classified as resistant. Living larvae on resistant plants of both durum and common wheat selections ranged in size, but generally were smaller (estimated to be mostly late first to early second instar) than larvae on susceptible plants of the same wheat selection. Larvae had developed to the flaxseed stage (late second to third instar) on most susceptible plants, but there were no flaxseed observed on resistant plants of any wheat selection.

Number of Genes Conditioning Resistance in 11 PI Lines

Data are summarized in Table 4. Check plants of the recurrent backcross parent D6647 were all susceptible,

Table 4. Backcross analyses of eleven germplasm lines of durum wheat for the number of genes conditioning resistance to Hessian fly biotype L at 19°C.

Backcross	Number of parent plants: Backcross parent R:S	Number of parent plants: Resistant parent R:S	Number of backcross families†: Seg. R & S	Number of backcross families†: All S	Segregation ratio tested	Adjusted Chi-square: Value	Adjusted Chi-square: Probability
D6647*2/PI 134942‡	0:47	46:2	64	26	3:1	0.7260	0.30–0.50
D6647*2/PI 166497	0:85	71:1	58	28	3:1	0.9399	0.30–0.50
D6647*2/PI 185410	0:79	56:0	48	42	1:1	0.2778	0.50–0.70
D6647*2/PI 185721	0:65	63:0	44	46	1:1	0.2778	0.50–0.70
D6647*2/PI 192351	0:90	77:0	61	29	3:1	2.1333	0.10–0.20
D6647*2/PI 192738	0:85	60:1	44	46	1:1	0.0110	0.70–0.80
D6647*2/PI 192839	0:76	60.0	69	21	3:1	0.0591	0.80–0.90
D6647*2/PI 192840	0:70	66:0	80	10	7:1	0.0573	0.80–0.90
D6647*2/PI 192851	0:56	134:1	53	37	1:1	2.5000	0.10–0.25
D6647*2/PI 274681	0:87	46:2	56	34	1:1§	4.8976	0.02–0.05
					3:1	7.1999	<0.01
D6647*2/PI 323440	0:91	62:0	48	41	1:1	0.4044	0.50–0.70

† Backcross F_2 families of 25 to 30 seedlings each.
‡ The designation D6647*2/PI 134942 indicates a cross of D6647 and PI 134942 and a cross of the F_1 back to D6647.
§ Also fits a model of two genes linked at 24 cM.

plants of the nonrecurrent parents were nearly all resistant, and plants of the Molly (*H*13) check (not shown) were all resistant. There was good precision in the 11 backcross analyses of the number of genes conditioning resistance in these durum germplasm lines.

PI 134942 and PI 166497 each appeared to have resistance to biotype L conditioned by two dominant genes (Table 4), giving a 3:1 backcross ratio. A single gene conditioned the resistance of PI 185410. Parent plants of PI 185410 were all resistant. Following infestation, resistant plants stunted like susceptible plants but regained growth and Hessian fly larvae died. The expression of resistance in plants heterozygous for resistance was calculated by means of the method for analyzing segregation for resistance within segregating backcross F_2 families. Plants of the PI 185410 parent were all resistant. Of a total of 1015 F_2 plants, 599 were resistant. After deducting one fourth or 254 parental resistant types, about 345 or about 68% of heterozygous plants expressed resistance.

The resistance of PI 185721 segregated in a backcross ratio indicating that a single dominant or partially dominant gene conditioned the resistance to biotype L. All plants of the resistant parent were resistant (Table 4). From a total of 782 F_2 plants in segregating families, 462 plants were resistant. After subtracting 195 calculated homozygous types, 267 or about 68% of the plants heterozygous for resistance expressed resistance. The backcross analysis of the resistance of PI 192351 indicated that resistance was conditioned by two dominant or partially dominant genes. All plants of PI 192351 were resistant. The resistance of PI 192738 in the backcross segregated in a good fit to a 1:1 ratio indicating a single dominant or partially dominant gene conditioned the resistance of PI 192738 (Table 4). Of a total of 984 F_2 plants within segregating families, 364 plants tested resistant. Of those, 118 or about 24% were calculated as heterozygous for resistance. All parent plants were resistant.

The backcross F_2 family analysis for PI 192839 indicated that resistance was conditioned by two dominant or partially dominant genes. All plants of PI 192839 were resistant (Table 4). PI 192840 appeared to have three genes segregating for resistance to biotype L. All plants of the resistant parent were resistant (Table 4). This parent and PI 192839 are recorded as having the same name (Table 2), but the difference in gene number for resistance is distinct in these analyses.

The resistance of PI 192851 appears to be conditioned by one dominant or partially dominant gene from the segregation of backcross families (Table 4). More than 99% of the parent plants were resistant. Of a total of 1050 F_2 plants within segregating families, 676 were resistant, with 414 or about 79% of the heterozygous plants calculated to express resistance.

Estimating the number of genes for resistance of PI 274681 was more puzzling. About 95% of the parent plants were resistant. The segregation of backcross F_2 families gave a poor fit to a 1:1 ratio and an unacceptable fit to a 3:1 ratio (Table 4). This may result from linkage of two genes calculated at about a 24-centimorgan separation.

The resistance of PI 323440 appeared to be conditioned by a single dominant or partially dominant factor. All plants of PI 323440 were resistant (Table 4). Plants of PI 323440 and resistant F_2 plants exhibited the stunting and growing out reactions described above for PI 185410. The two lines have different recorded areas of origin (Table 2). There were 928 F_2 plants in the segregating backcross families of which 522 were resistant. This leaves a calculated 290 or about 65% of the heterozygous F_2 plants that expressed resistance.

DISCUSSION

Expression of Resistance in Durum and Common Wheat

Most genes for resistance to Hessian fly from durum wheat function effectively when transferred to common wheat genotypes, but there are exceptions. Obanni et al. (1989) observed that the *H*5 gene for resistance was expressed at a somewhat higher temperature in durum than in common wheat. Genes *H*6, *H*11, and *H*16 derived from PI 94587 durum expressed well when added to Newton and some other common wheats. In the present test, resistance gene *H*16 functioned effectively in both common and durum wheat lines, although the expression of resistance was higher in the durum wheat line to the Delaware population (Table 3). Data were not obtained for the response of P921682A4 to the Georgia population, as described in Results. In previous testing (unpublished data, 2000), the *H*16 gene in the same common wheat line (P921682A4) expressed moderate resistance (85, 80, and 78% resistant plants) to fly populations from Florida, Indiana, and South Carolina; however, there was not a durum source of *H*16 resistance in the test for comparison.

The susceptibility of PI 428435 (*H*17) was unexpected because resistance (95–100%) to fly populations from Maryland was observed in previous tests with *H*17 in the same durum line (Ratcliffe et al., 1994). However, tests reported by Ratcliffe et al. (1994) were conducted with fly populations collected in Maryland in 1989. Changes within Maryland populations for the relative frequency of virulence genes occurred during this time. The two populations tested by Ratcliffe et al. (1994) and the population tested by us (Table 1) were collected from the same general area of the Eastern Shore of Maryland; however, the frequency of biotype L was much higher in the 1999 (96%) than the 1989 populations (35 and 54%). Ratcliffe et al. (1994) reported that virulence to gene *H*9, which confers resistance to biotype L, differed among fly populations that were classified as predominately biotype L but were collected from different geographical locations in the eastern USA. As noted by Ratcliffe et al. (1994), biotype L, as identified in tests reported here, is defined by the ability to infest all of the four differential hosts with the wheat genes *H*7*H*8, *H*3, *H*5, and *H*6. However, biotype L may be represented not by a single virulence gene but by several different virulence genes (Ratcliffe et al., 1994). Similarly, although *H*17 is resistant to biotype L, it is possible that virulence to *H*17 within populations composed

largely of biotype L may differ and that the reduced effectiveness of *H*17 that we observed may be related to the increase in frequency of biotype L in fly populations from this area of Maryland. This possibility illustrates the importance of evaluating new resistance genes for response to current geographical populations of the Hessian fly, as well as laboratory biotypes, when making decisions on genes to incorporate into common wheat cultivars.

Caldwell et al. (1946) observed the presence of low numbers of living larvae on plants carrying resistance from 'Illinois No. 1'W38 (*H*3) but these plants demonstrated no symptoms of infestation (phenotypically resistant). They reported that a large proportion of the puparia on these resistant plants were abnormally small or contained dead larvae. These authors also observed the capacity of some plants that contained larvae to recover from slight stunting; this response was seen particularly when tests were conducted in the field or greenhouse at temperatures above 20°C. Caldwell et al. (1946) described resistance in this material both as the plants' capability to prevent larval development under conditions favorable for the expression of resistance as well as to grow normally, although infested, under less favorable conditions. In both cases, plants expressed effective levels of resistance to Hessian fly. Recovery after stunting was observed in some plants of PI 185410 and PI 323440, when tested to biotype L at 25°C (Cambron, Ohm, Patterson, unpublished data, 1995), but this response was not observed in any of the PI lines to any of the fly populations in tests reported here at 18°C.

Genetic Plant Necrosis Problems

There are three plant necrosis genotypes, Ne_1Ne_1 ne_2ne_2, ne_1ne_1 Ne_2Ne_2, and the double recessive. When crosses are made between the two dominant genotypes, the heterozygous plant develops leaf necroses at about the three- or four-leaf stage and usually dies before reproduction. There are several Ne-alleles described by Zeven (1971) as weak, moderate, or strong. Many of the durum wheat sources resistant to Hessian fly come from regions where Ne_1 genes predominate although noncarriers (double recessives) also occur (Zeven, 1971). Ne_2 carriers predominate among wheat cultivars in the eastern, soft red winter wheat region of the USA.

In using unknown Ne-gene genotypes in a genetic or breeding study, one is prudent first to make one or two crosses to a noncarrier type before crossing to a line which may be a carrier of Ne_1 or Ne_2. In our genetic research at the durum level, we have used the spring semidwarf durum germplasm line North Dakota D6647 (CI 15329, Lebsock et al., 1972) as the recurrent parent in backcross and testcross analyses of resistance to Hessian fly. We found it to be a noncarrier of dominant Ne-genes and susceptible to all biotypes of Hessian fly to which it has been tested. The semidwarf height results in better standing ability in greenhouse culture.

In genetic studies with common wheat, we found that winter wheat cultivars Newton (CI 17715) and Knox (CI 12798) were noncarriers of dominant Ne-alleles and were susceptible to all biotypes of Hessian fly to which they were tested. Recently, R. H. Busch (see acknowledgments) suggested the spring wheat cultivar Len (CI 17790) as a noncarrier. We found it to be susceptible to all biotypes of Hessian fly that we maintain. As a spring wheat recurrent parent, we can cycle more generations per year than with winter wheat cultivars.

Utilizing Resistance from Durum Wheat

There appear to be many potentially useful sources of resistance to the changing populations of Hessian fly in eastern USA among the 26 durum wheat lines observed in our tests. The lines with resistance conditioned by single genes could be utilized more quickly.

We believe that the most effective approach for using genes for resistance to Hessian fly from these durum germplasm lines is to isolate single genes conditioning resistance in durum or common wheat so that the resistance can be thoroughly studied for effectiveness against different biotypes and populations of Hessian fly. The identification of markers for the genes would provide efficient and practical tools for pyramiding two or more genes in a cultivar to provide long-term effectiveness of the resistance to Hessian fly. DNA markers for eleven genes for resistance are available, including one for the very effective *H*13 (Dweikat et al., 1997). Since the effectiveness of a gene for resistance to Hessian fly is sometimes somewhat different in durum and common wheat, preference for the analysis should be at the ploidy level of anticipated use in breeding resistant cultivars.

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